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HABITAT RELATIONSHIPS OF SUBADULT HUMPBACK CHUB IN THE COLORADO RIVER THROUGH GRAND CANYON: SPATIAL VARIABILITY AND IMPLICATIONS OF FLOW REGULATION

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ABSTRACT

We examined subadult humpback chub densities along 24 kms of the Colorado River in the Grand Canyon to: (1) identify geomorphic conditions in the study area; (2) determine associations between subadult humpback chub (< 200 mm TL) habitat use and geomorphic differences; and (3) determine how discharge, during base flow conditions, was related to subadult humpback chub habitat conditions.

Habitat was categorized at two nested spatial scales: geomorphic reach and shoreline type. Within reaches, shoreline types were categorized according to geomorphology. We measured water depth, velocity and cover attributes along all shoreline types over a range of discharges to determine if habitat quality of reaches and shoreline types varied with discharge.

Reaches 1 and 3 had narrow, deep corridors, whereas Reach 2 was a wide, shallow reach. Among shoreline types, depth, velocity and cover varied; however, differences were not consistent between reaches. Fish densities also varied among shoreline types and reaches. Vegetation, talus and debris fan shorelines had the highest densities of subadult humpback chub in a pattern similar to that of cover. In addition, subadult humpback chub presence was associated with a high frequency of cover regardless of shoreline designation. However, these relationships explained little of the overall variation in subadult densities.

Lack of a strong association between fish density and geomorphology may be partially due to effects of discharge on habitat quality. The overall trend among shorelines (without regard to type) showed that cover decreased with increasing discharge, whereas depth and velocity increased. However, no consistent pattern between discharge and depth, velocity and cover among individual shoreline types was evident.

Vegetated shorelines, consisting mainly of non-native tamarisk (*Tamarix chinensis*), had nearly twice the fish densities of talus and debris fan. Reasons are discussed as to why subadult humpback chub occupy naturalized habitat like vegetated shorelines in greater densities than natural habitats. The relationships observed in this study have important implications for humpback chub recovery and management of the Colorado River through Grand Canyon. © 1998 John Wiley & Sons, Ltd.

KEY WORDS: humpback chub; habitat; geomorphology; shoreline; cover; flow; regulation; Colorado River; Grand Canyon

INTRODUCTION

In 1967, the US Fish and Wildlife Service (USFWS) listed the humpback chub (*Gila cypha*) as endangered following a decline in numbers in the Colorado River (Minckley, 1991). Federal listing prompted a number of studies to describe the ecology and determine the status of humpback chub (Vanicek *et al*., 1970; Holden and Stalnaker, 1975; Carothers and Minckley, 1981; Valdez and Clemmer, 1982; Kaeding and Zimmerman, 1983; Berry and Pimentel, 1985; Miller and Hubert, 1990; Valdez *et al*., 1992). However, humpback chub are difficult to study because of their rarity and their residence in swift, turbid and inaccessible riverine environments; as a result, 25 years of investigation has yielded little information on this fish, particularly at early life-history stages (Gorman *et al*., 1994; Valdez and Ryel, 1995).

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In this study, the physical environment of subadult humpback chub and how habitat was related to discharge during base-flow conditions is examined. This study was developed to address three objectives: (1) identify geomorphic differences among reaches and among shoreline types within reaches; (2) determine if subadult humpback chub were associated with these geomorphic differences; and (3) determine how discharge, during base flow conditions, affects subadult humpback chub habitat conditions.

Biology and status of the humpback chub

Historically, humpback chub were thought to have ranged throughout the Colorado River system in swift canyon reaches that are now inundated or decimated by water development projects. Presently, six known populations occur in canyon reaches. The largest and most stable population resides in the Colorado River in Grand Canyon in and near the Little Colorado River (LCR). Successful spawning occurs only in the LCR (Valdez and Hugentobler, 1993). This is the only population remaining below Glen Canyon Dam (US Fish and Wildlife Service, 1990).

In 1978 the USFWS determined that the operation of Glen Canyon Dam was likely to jeopardize the continued existence of the humpback chub in Grand Canyon. Consequently, the USFWS required an investigation of the effects of dam operations on the resources of Grand Canyon, including the endangered humpback chub. One result of these studies was the implementation of interim flow operating criteria (interim flows) in August 1991 to reduce the effects of fluctuating flows. A second result of the GCES studies was implementation of an ecological assessment of the humpback chub in Grand Canyon (Valdez *et al*., 1992).

These studies have yielded valuable information on the ecology of this species, and the USFWS has assimilated findings from ongoing humpback chub studies into the Glen Canyon Dam Environmental Impact Statement (US Department of Interior, Bureau of Reclamation, 1995). However critical aspects of the ecology of humpback chub remain unclear. The endangered status of humpback chub requires that operations of Glen Canyon Dam (GCD) are conducive to the recovery and sustainability of this population. Dam operations directly affect the Colorado River in Grand Canyon through changes in flow, temperature, sediment transport and vegetation dynamics (Stanford and Ward, 1991). To date, most of the scientific and political concern regarding flow regime has centered on the magnitude and timing of peak flows, as exemplified by the experimental flood in Grand Canyon in spring of 1996 (Collier *et al*., 1997).

We contend that although peak flows are important for sediment transport, habitat maintenance, and perhaps environmental spawning cues, base flows, which occur in the Colorado River through the Grand Canyon 7–10 months of the year, are also important to the maintenance of resident fish populations. Yet, this aspect of the flow regime has been largely ignored. The relationship between habitat condition and base flows should be examined and better understood before operation of GCD is decided. In this study, we examine the relationship between base flows, habitat condition and habitat use by early life-history stages of humpback chub.

STUDY AREA

Hydrology and management

This study took place in a 24-km reach of the Colorado River that flows through Grand Canyon beginning at the confluence with the LCR (Figure 1). Hydrology of the Colorado River through Grand Canyon is regulated by Glen Canyon Dam, approximately 25 km upstream of Lee's Ferry, Arizona. For consistency with published maps, river distances refer to river miles (RM) below Lee's Ferry (Belknap and Evans, 1989). RM is the standard distance metric used in Grand Canyon to describe location (Valdez and Ryel, 1995).

Historically, the Colorado River was a highly turbid, highly fluctuating system. Temperature varied seasonally from near freezing to almost 30°C. Flows could range annually from approximately 60 $m^3 s^{-1}$ during winter months to over 3000 $m^3 s^{-1}$ (US Department of Interior, Bureau of Reclamation, 1995). The dam has altered the hydrology of the river by eliminating large annual flood events, maintaining artificially high base flows, trapping sediment and altering physio-chemical conditions (Stanford and Ward, 1991). Water discharged from the dam is approximately 7–11°C and warms an average of 1° every 50 km downstream in the summer (Valdez and Ryel, 1995).

From the period of dam closing in 1962–1991, discharge fluctuated within a range of 60–850 $m^3 s^{-1}$ with unrestricted ramping rates. To reduce these fluctuations, the USBR implemented interim flows in August 1991. This operating regime requires a minimum of 225 $m^3 s^{-1}$ and a maximum of 550 $m^3 s^{-1}$. Up ramping (rate of discharge increase) does not exceed 70 $m^3 s^{-1} h^{-1}$, and down-ramping (rate of discharge decrease) does not exceed 45 $m^3 s^{-1} h^{-1}$ (US Department of Interior, Bureau of Reclamation, 1995).

Within the Grand Canyon, the study area begins at the confluence of the Colorado River with the LCR (RM 61.4), a calcium carbonate-enriched, spring-fed tributary to the Colorado River in Grand Canyon (Figure 1). The LCR flows clear except during heavy, upland rainstorms when it floods and becomes sediment laden. With a base flow of 5.5 $m^3 s^{-1}$ and a 10-year recurrence interval flood of 425 $m^3 s^{-1}$, the LCR is the largest tributary entering the Colorado River in Grand Canyon.

Geomorphology

Grand Canyon is the result of concurrent uplifting of the Colorado Plateau and down cutting of the Colorado River through more than 1500 m of sedimentary and metamorphic rock (Beus and Morales, 1990). The river through Grand Canyon drops over 500 m in 450 km (279 miles) as a series of long, flat stretches interrupted by steep drops. Half of the drop in elevation is in rapids, which constitute only 9% of the total distance. Most of the rapids are formed by debris fans at the mouths of ephemeral tributaries that deposit poorly sorted debris ranging in size from huge boulders to sand. These debris fans occur where local fractures or faults transect the canyon at the river (Dolan and Howard, 1978). Debris flows and tributaries deposit enough sediment to constrict the river, forming rapids. Associated with rapids are large downstream zones of recirculation known as eddy complexes (Schmidt and Graf, 1990).

Channel slope and morphology in Grand Canyon change along the river corridor with shifts in local geology and tributary influence (Leopold, 1969; Kieffer, 1990). More resistant lithology creates a narrow,

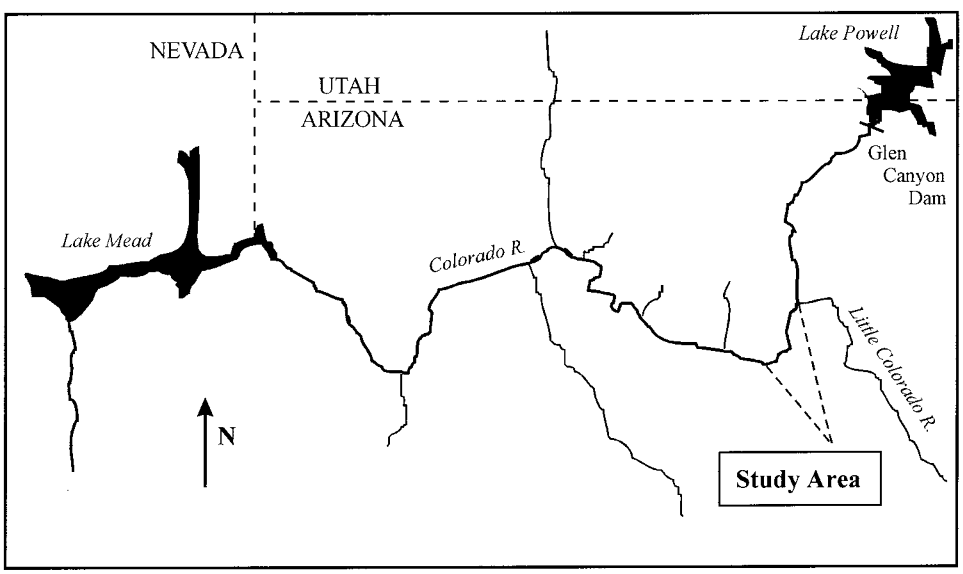

Figure 1. Map of the Colorado River through Grand Canyon

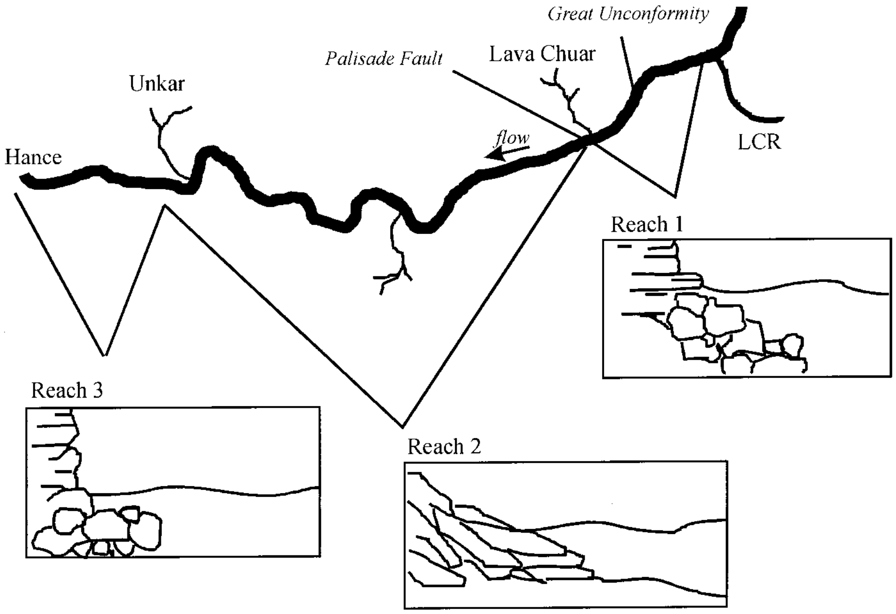

Figure 2. Map of the study area showing geomorphic reaches

deep corridor, whereas it is wider and shallower in regions of locally erodible lithology (Howard and Dolan, 1981). These changes are used to designate three contiguous reaches in the study area (Figure 2).

Reach 1. In reach 1, Tapeats Sandstone dominates the geology at the river surface where the LCR flows into the main channel (RM 61.4). Tapeats is a medium to coarse-grained sandstone (Middleton and Elliot, 1990). Layers are differentially eroded but generally resistant which causes characteristic ledges and cliffs 30–100 m above the river surface in a narrow corridor (Middleton and Elliot, 1990).

Below RM 63, the geology shifts to the Dox Formation consisting of: Ochoa Point, Comanche Point, Solomon Temple and Escalante Creek in descending order. Because these underlying strata are tilted, the lower Escalante Creek member of Dox Formation is the first Dox strata encountered at river level. This cliff forming layer maintains the narrow river corridor (Hendricks and Stevenson, 1990).

Reach 2. At Lava Chuar Canyon (RM 65.5), the river crosses the Palisades Fault. Here, geologic strata are displaced, and upper, more erodible members of Dox Sandstone emerge at river level. The river is shallower and the corridor widens as the river cuts into the shaley, more erodible Ochoa Point, Comanche Point and Solomon Temple members of Dox Formation (Billingsley and Elston, 1989). The channel continues as such to below Unkar Rapid (RM 73.4).

Reach 3. Below Unkar Rapid, the Escalante Creek member resurfaces (Billingsley and Elston, 1989) and the river channel narrows again continuing as such through resistant Shinumo Quartzite (RM 75.4). Hakatai Shale dominates the shoreline at RM 76, about 1 km upstream of Hance Rapid (RM 76.5). The brief emergence of the erodible shale does not affect the channel morphology, and the corridor remains narrow through the end of the study area at Hance Rapid (RM 76.5).

METHODS

Study design

This study was one component of a larger project that focused on the ecology of the humpback chub in the Colorado River through Grand Canyon (Valdez and Ryel, 1995). To address the objectives of this study, three types of data were collected at two nested spatial scales: reach and shoreline. First, we

Table I. Definitions of shoreline types

Bedrock	Any rock that is in its original location and has not been transported or broken up by any means. This includes shear walls and laterally or vertically emerging ledges
Cobble	Rocks transported by main channel activity that are characteristically well rounded and imbricated. They may show some embeddedness
Debris fan	Debris, predominantly boulder, transported from a tributary during a flooding event. It is characterized by boulders with some degree of embeddedness, intermittent sand beaches, and a small percentage of gravel. The angle of repose is generally flatter than that of talus. The boulders are more rounded as inferred by the process of transportation
Sand	Minimum length of 50 m of predominantly exposed sand. Beaches can have very steep banks or be very flat
Talus	Colluvium, predominantly boulder, deposited by rockfall or rockslide activity on the canyon walls. It is characteristically not embedded and has a steeper angle of repose than a debris fan. May have some intermittent sand. Debris is more angular as inferred by its process of transportation
Vegetation	This can be rooted or inundated vegetation. The vegetation along the shoreline must be in or directly over the water on the shoreline. Vegetation may have intermittent stretches of other shoreline types

quantified physical habitat conditions for six shoreline types within two reaches (reaches 1 and 2). Shoreline type designations, based on differences in structure and geomorphology, included bedrock (shelves and vertical cliffs), cobble, debris fan, sand, talus and vegetation (Table I). Second, we used stratified random sampling to estimate relative fish densities in all six shoreline types within all reaches (reaches 1, 2 and 3). Reach 3 was added to this analysis midway through the study after habitat data collection was completed, hence we were only able to obtain fish capture data from reach 3. Finally, data were collected on discharge variability and how habitat changed as a consequence of flow variation was estimated. Both physical measurements and fish sampling were conducted over the range of discharges from Glen Canyon Dam that represented interim flows. Data collection was conducted for 1–2 weeks per month from October 1990 to November 1993 (except Decembers) and in July 1994 (Valdez and Ryel, 1995).

To determine geomorphic differences among reaches, we calculated total availability of shoreline types, total riffle area and width-to-depth ratios of reaches 1, 2 and 3. To quantify differences in habitat at both spatial scales (reach and shoreline), water depth, velocity and cover along shorelines were measured within reaches 1 and 2.

Because reach 3 was added midway through the study, shoreline habitat data were collected in reaches 1 and 2 only. Physical habitat sample sites were stratified among reaches 1 and 2 to include all shoreline types but were randomly chosen within reaches. Because we were logistically limited in where, when and how often certain data could be collected, sample numbers among reaches and shoreline types were not balanced (Table II). Fish sampling was stratified among the six shoreline types and randomly chosen within all three reaches. A total of 664 electrofishing efforts conducted (Table III) were used to summarize habitat conditions, however only 173 electrofishing samples that had spatially concurrent habitat measurements were used to analyze direct associations of fish with habitat.

Table II. Number of transects measured among reaches and shoreline types

Reach	Shoreline type						Total
	Bedrock	Cobble	Debris fan	Sand	Talus	Vegetation	
1	4	2	7	11	7	9	40
2	3	7	2	3	7	7	29
Combined	7	9	9	14	14	16	69

Table III. Number of electrofishing samples among reaches and shoreline types

Reach	Shoreline type						Total
	Bedrock	Cobble	Debris fan	Sand	Talus	Vegetation	
1	69	21	92	36	164	63	445
2	27	15	20	7	49	56	174
3	2	2	5	4	12	20	45
Combined	98	38	117	47	225	139	664

To account for changes in habitat condition and habitat use with discharge, we used discharge data from two USGS gauge stations. For analysis of physical habitat changes within the study area, discharge data from the gauge station located above the confluence of the LCR were used (station number 9383100). The discharge at this station most closely reflected the actual discharge within the study area at the time of data collection.

For analysis of long-term changes in the overall flow regime, data from the gauge station located at Lee's Ferry was used (station number 9380000), because this station maintained the longest period of record. We used the latter data to derive flow duration curves (see Data collection) for pre- and post-dam periods of the Colorado River in Grand Canyon, which allowed us to compare differences in the flow regime since construction of Glen Canyon Dam.

Data collection

Geomorphic reaches. To quantify differences in reach geomorphology, the total length of each of the shoreline types and surficial riffle area along the entire 24-km study area was mapped and the mean width-to-depth ratios of each reach was calculated. Surficial riffle area was defined as a relatively shallow area that was characteristically broken or rippled by fast water moving over underlying cobble but that lacked standing waves. The total available shoreline of each type was mapped on mylar overlays of 1:24000 scale aerial photographs. The percentage riffle area in reaches was then mapped and shoreline mapping was verified in the field. The channel transect data of Schmidt and Graf (1990) taken at arbitrary cross sections throughout the study area were used to derive an average width-to-depth ratio for the three geomorphic reaches.

Shoreline longitudinal transects. Three habitat variables along 100 m lengths within different shoreline types were quantified. We refer to one set of measurements as a longitudinal transect. At each 10-m interval along a transect, water depth and water velocity were measured (at 0.6 of depth) and the presence of cover types was recorded. We assumed that shoreline structure most strongly influenced channel hydraulic conditions within 2.5 m of the shoreline and, therefore, measured depth, velocity and cover at three distances from shore: 0.5, 1.5 and 2.5 m. The presence of three cover types was recorded: lateral (L), instream (I) and overhead (O) (Table IV). Cover was based on lateral, emergent or overhead shelter from hydraulic or visual exposure. We tallied the presence of each cover type at each point, and then summarized the frequency of cover for each longitudinal transect. Each longitudinal transect comprised

Table IV. Definition of cover types

Cover type	Definition
Lateral	Any laterally emerging instream structure that obstructs flow and provides shelter from the main current above, below or beside it
Instream	Any instream structure emerging vertically from the river bottom that obstructs flow and provides shelter from the current in its wake
Overhead	Any structure from the shore that hangs above the water in the channel margins

90 data points: three variables (depth, velocity and cover), three distances from shore at 10-m intervals along 100 m of shoreline. With these data, mean transect depth, velocity and total cover were derived for reaches 1 and 2 and for all six shoreline types. A total of 69 longitudinal transects among all shoreline types were measured: 40 in Reach 1, and 29 in Reach 2 (Table II). Discharge at the time transects were obtained from the gauge station located above the confluence of the LCR.

Fish sampling. We used electrofishing catch rates to estimate relative densities of subadult humpback chub (< 200 mm TL) within all three geomorphic reaches and each of the six shoreline types (Table III). Electrofishing was conducted from Achilles SU-16 research boats equipped with Mark XX® Complex Pulse Systems, as described in Valdez and Ryel (1995). The time required to sample each shoreline was recorded, and catch per unit effort (CPE) was expressed as the number of fish caught per 10 h of fishing. A 1:1 time:area fish-sampling ratio was assumed and thus the catch data were used as a measure of relative density. Time of day and turbidity were recorded for each sample (Valdez and Ryel, 1995). Only samples from high turbidity, nighttime or crepuscular periods were used to reduce confounding effects of light on catch rates (Valdez and Hugentobler, 1993).

Flow duration curves. We used mean daily discharge data from the Lee's Ferry gauge to derive pre- and post-dam flow duration curves. Flow duration curves characterize the temporal flow regime by showing the temporal flow distribution as a discharge occurring over a percent of time for a period of record (Leopold *et al*., 1964). Data from 1922 and 1960 were used to construct the pre-dam curve and from 1965 and 1994 to construct the post-dam curve. To construct these curves, discharge was ranked from highest to lowest and plotted against cumulative percent time.

Analyses

Physical differences among geomorphic reaches and shoreline types. Our first objective was to quantify physical differences among reaches and shoreline types. To determine how reaches were geomorphically different, the availability of shoreline types, width-to-depth ratio and total riffle area of the three reaches were examined. To determine if depth, velocity and cover varied between reaches (blocks) and among shoreline types (treatments) and to determine if shoreline conditions depended on reach (interaction), a generalized randomized block multiple analysis of variance was used (GRB MANOVA) (Neter and Wasserman, 1974). Because we were specifically interested in physical differences among only these reaches and our inferences would be limited to this system, we considered the reach effect as fixed. This assumption allowed us to use the residual error term as the mean square error when calculating F-ratios (Neter and Wasserman, 1974). Mean transect depth and velocity were $\log_{10}$-transformed to correct for heteroscedasticity in the MANOVA (Zar, 1984). We used an *a priori* α value of 0.1 (10% chance of type I error) for all statistical analyses due to low sample size and probable low power.

Relationships between subadult humpback chub and geomorphology. To determine if subadult humpback chub were associated with reach and shoreline differences (objective 2), associations of fish with specific depth, velocity and cover conditions were examined and relative densities of fish among reaches and shoreline types were compared. Initially, we wanted to determine if the longitudinal distribution of subadult humpback chub could be explained by something other than habitat selection (e.g. passive dispersion). We therefore examined how densities varied throughout the three reaches for each shoreline type. Downstream distributions of subadult humpback chub densities within each shoreline type were fitted with a LOWESS line-of-best-fit (SYSTAT, Inc., 1992). A monotonic decline in density would be consistent with the distribution expected from passive dispersion. A flat line with large differences in magnitude of densities among shoreline types would imply local habitat selection was occurring.

Discriminant functions analysis (DFA) was used to determine if the presence of fish within sample units was associated with differences in mean depth, velocity and cover. For this analysis, only fish samples that were spatially concurrent with a longitudinal transect ($n = 173$) and thus had associated habitat information were used.

To determine if variation in fish densities was associated with differences among reaches or shoreline types, a GRB ANOVA was conducted with reaches as blocks and shoreline type as the treatment. An interaction term between reach and shoreline type was included in this model. Block effects were also

Table V. Width to depth ratios (W:D) measured at arbitrary cross sections (Schmidt and Graf, 1990) summarized by reach

Reach	RM	W:D	Average W:D
Reach 1	62	20.7	
	63.4	16.8	
	64.1	21.7	
	65	19.2	19.6
Reach 2	67.1	13.6	
	67.8	66.5	
	68.2	31.6	
	70.2	20.6	
	70.7	24.1	
	71.2	29.6	
	71.8	49.7	
	73.5	36.9	34.0
Reach 3	73.8	13.2	
	74.2	20.1	
	74.6	19.2	
	76.1	15.4	17.0

considered fixed in this analysis. Densities of subadult humpback chub were $\log_{10}$-transformed to correct for heteroscedasticity (Zar, 1984).

To compare the total abundance of subadult humpback chub among reaches, the mean fish densities along specific shoreline types were multiplied by the length of each shoreline in a reach.

Effects of flow regime changes on habitat conditions. To assess how changes in flow regime may have affected habitat conditions (objective 3), we first examined changes in habitat condition associated with discharge and then examined how the temporal flow regime has been altered by flow regulation. A multivariate simple linear regression (MSLR) was used to determine if habitat conditions (mean depth, velocity and cover) changed over the range of interim flow discharges. Separate tests for effects of discharge, shoreline type and the interaction between discharge and shoreline type on habitat condition were conducted. Colorado River flow duration curves for pre- and post-dam periods were compared to examine flow regime changes and to assess the overall effect of flow regulation on habitat conditions.

RESULTS

Physical differences among geomorphic reaches and shoreline types

Reaches 1 and 3 were geomorphically similar and differed from reach 2 in that the width-to-depth ratio was nearly two times greater in reach 2 (Table V). Percent total riffle area was three to five times greater in reach 2 (21%) than in reach 3 (6%) or reach 1 (4%), respectively. These results led us to suspect that either the distribution of or the physical condition of shoreline types may be influenced by reach. In fact, although habitat conditions appeared to vary significantly both among shoreline types and between reaches, a significant interaction between reach and shoreline type suggested differences among shoreline types were not consistent between reaches (Table VI, Figure 3).

Univariate tests showed that this interaction was largely influenced by substantial differences in depth and cover between bedrock shorelines in reaches 1 and 2. For example, in reach 1, mean depth of bedrock shorelines (2.39 m) was clearly different from that of all other shoreline types (0.30–1.0 m), whereas in reach 2, depths of all shoreline types were more uniform (0.25–0.60 m) (Figure 3). Also, in reach 2, bedrock shorelines had a high frequency of cover, whereas cover was high in debris fan, talus and vegetated shorelines in both reaches 1 and 2, and cover was low in cobble and sand shorelines in both reaches 1 and 2 (Figure 3).

Table VI. Results of generalized, randomized block MANOVA for mean depth, velocity and cover among shoreline types and reaches (for reaches 1 and 2 only). DF, degrees of freedom

Source	DF	Wilks' λ	F	p
Shoreline (S)	15, 152	0.198	8.09	<0.001
Reach (R)	3, 55	0.611	11.68	<0.001
$R \times S$	15, 152	0.554	2.42	0.003

Relationships between subadult humphack chub and geomorphology

Fish densities did not monotonically decline from upstream to downstream or show any other recognizable pattern; however, mean relative density varied substantially among shoreline types (Figure 4). In addition, other species, such as speckled dace, not reported here, differed in habitat use and relative abundance from that of subadult humpback suggesting that sampling efficiency bias among shoreline types was minimal (Valdez and Ryel, 1995). These results imply that subadults were quickly dispersing and then preferentially using specific shoreline types along the river corridor while avoiding others. Discriminant functions analysis showed that subadult humpback chub used locations that were physically different than unoccupied areas (Table VII). Areas with fish had more cover ($p < 0.001$) and lower velocity ($p = 0.10$) than those without but did not differ significantly in depth ($p = 0.84$).

Estimates of overall fish abundance, based on shoreline availability and shoreline use, were highest in reach 3 (82 fish caught per 10 h of fishing), intermediate in reach 1 (50 fish caught per 10 h fishing) and lowest in reach 2 (33 fish caught per 10 h fishing). However, a GRB ANOVA showed a significant interaction between reach and shoreline type, suggesting that the pattern of shoreline selection varied between reaches (Table VIII).

Overall, densities were highest in vegetated shorelines, followed by talus and debris fan shorelines. Bedrock, cobble and sand shorelines had low densities of subadults. However, when considering the interaction with reach, relative densities in bedrock shorelines in reach 2 were high compared with bedrock shorelines in reaches 1 and 3, whereas relative densities in talus shorelines in reach 2 were low

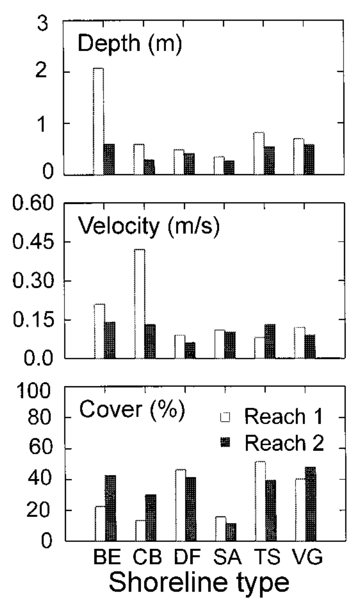

Figure 3. Physical differences in depth, velocity and cover among shoreline types and between Reaches 1 and 2. Be, bedrock; CB, cobble; DF, debris fan; SA, sand; TS, talus; and VG, vegetation

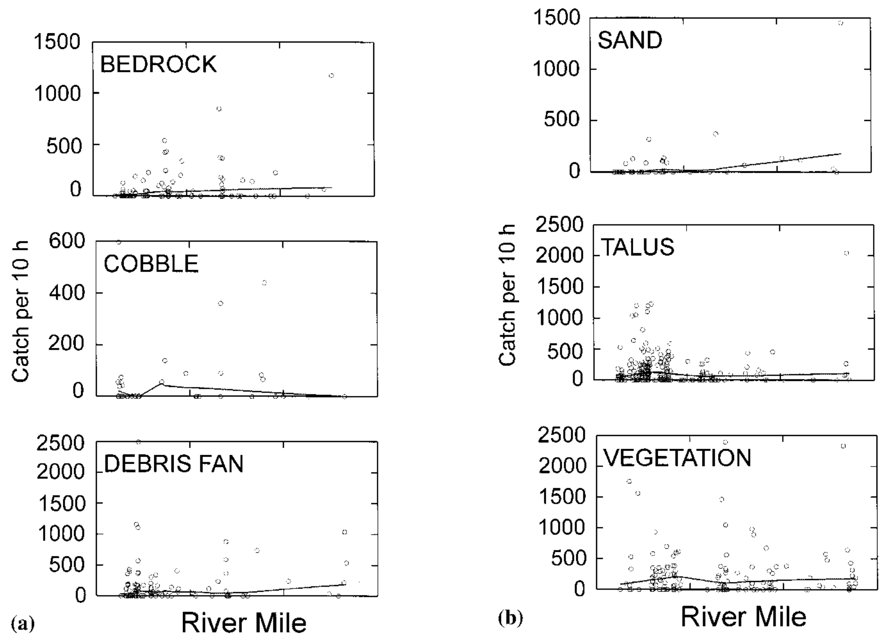

Figure 4. Downstream distribution of individual electrofishing samples for bedrock, cobble, debris fan, sand, talus and vegetation shoreline types

compared with reaches 1 and 3. This pattern of habitat use was similar to patterns of cover frequency among shoreline types (compare Figures 3 and 5). Shorelines with the highest relative densities within reaches also had the highest frequencies of cover, and cover was also the main factor associated with fish presence (Table VII). Subadult humpback chub appeared to be associated with certain physical conditions of cover, yet the relationship between reach and shoreline geomorphology and fish densities explained only 12% of the overall variation in fish densities.

Table VII. Results of the discriminant functions analysis. UFP, p value for univariate F-test. MV, results of multivariate test

Variable	Fish	No fish	UFP	Wilks' λ	p
Depth (m)	2.61	2.67	0.84		
Velocity (m s^{-1})	0.11	0.13	0.10		
Cover (%)	43	33	<0.001		
MV				0.89	<0.001

Table VIII. Results of 2-way ANOVA showing differences in subadult humpback chub densities among reaches and shoreline types in Figure 5

Source	DF	MS	F	p	r^2
Shoreline (S)	5	6.249	5.366	<0.001	0.12
Reach (R)	2	0.148	0.126	0.88	
$R \times S$	10	2.083	1.776	0.06	
Error	642	1.173			

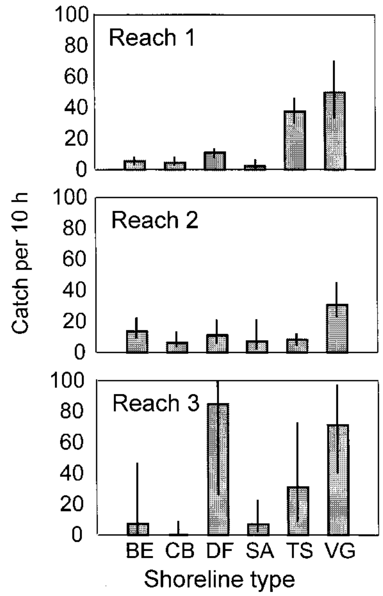

Figure 5. Relative densities of subadult humpback chub among shoreline types in reach 1, reach 2 and reach 3. Be, bedrock; CB, cobble; DF, debris fan; SA, sand; TS, talus; and VG, vegetation

Relationship between discharge and habitat condition

The MSLR showed that habitat conditions varied significantly with discharge for certain shoreline types (Table IX). Overall, mean shoreline depth and velocity increased with increasing discharge, whereas mean cover decreased (Figure 6). However, this trend was not consistent among shoreline types. Mean depth and velocity of bedrock, debris fan, cobble and vegetation shorelines tended to increase with increasing discharge, whereas they decreased within sand and talus shoreline types (Figure 7). Total cover within bedrock, talus and debris fan shorelines decreased with increasing discharge, yet total cover within cobble, sand and vegetation shorelines remained constant or increased.

When considered in conjunction with changes in the discharge regime, these results suggest that habitat quality has decreased in the post-dam era. A comparison of the flow duration curves for the pre- and post-dam periods show that the temporal distribution of discharge has changed such that mean daily discharges are less extreme more of the time (Figure 8). Prior to dam closure, discharge was less than 140 $m^3 s^{-1}$ 20% of the time and less than 225 $m^3 s^{-1}$ more than 50% of the time. Since construction of Glen Canyon Dam, flows less than 140 $m^3 s^{-1}$ have occurred only 3% of the time, and flows less than 225 $m^3 s^{-1}$ have occurred only 12% of the time.

Table IX. Results of multivariate simple linear regression showing changes in depth, velocity and cover with discharge. DF, degrees of freedom of the numerator and denominator

Source	DF	Wilks' λ	F	p
Discharge (Q)	3, 55	0.539	15.69	<0.001
Shoreline (S)	15, 152	0.359	4.56	<0.001
Q × S	15, 152	0.366	4.46	<0.001

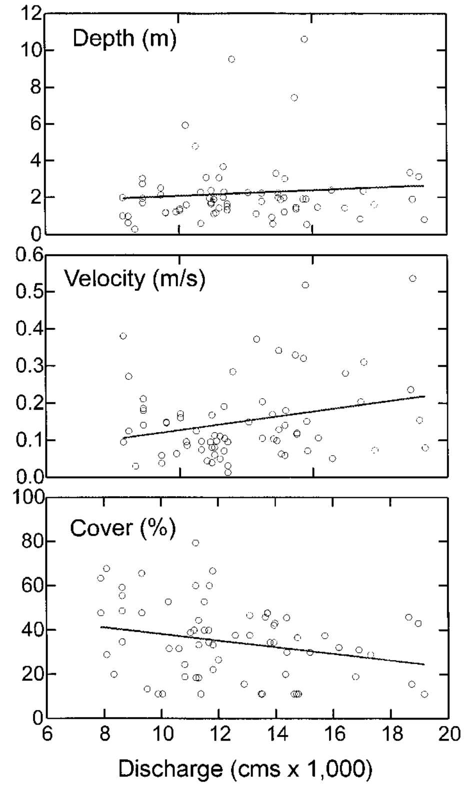

Figure 6. Overall change in depth, velocity and cover with discharge. All shoreline types are included in each graph

DISCUSSION

Relationships between humpback chub and geomorphology

Because of the strong influence of geology on the Colorado River ecosystem and the endemic nature of the native fish community, relationships between aquatic habitat and river geomorphology must be understood to manage in a manner which is sympathetic for the welfare of resident fish populations. These relationships seem particularly important to the humpback chub because of its apparent strong evolutionary and ecological ties to geomorphic structure at different life-history stages and different spatial scales (Valdez and Clemmer, 1982; Valdez and Ryel, 1995). In a different region, Rabeni and Jacobson (1993) found a similar relationship. They determined that centrarchid distribution in Ozark streams was influenced by geomorphology on a reach scale and velocity, depth and substrate at a local scale.

In this study, we showed that reaches and shoreline types differed physically and that subadult humpback chub presence and abundance in Grand Canyon were related to these geomorphic differences, particularly among shoreline types. This study also demonstrated that subadult humpback chub were specifically associated with a high frequency of cover in channel margins. In fact, the pattern of fish distribution and abundance among shorelines parallels the frequency of cover among shorelines, with vegetation, talus and debris fan shorelines having more cover and greater fish densities than bedrock, cobble and sand shorelines.

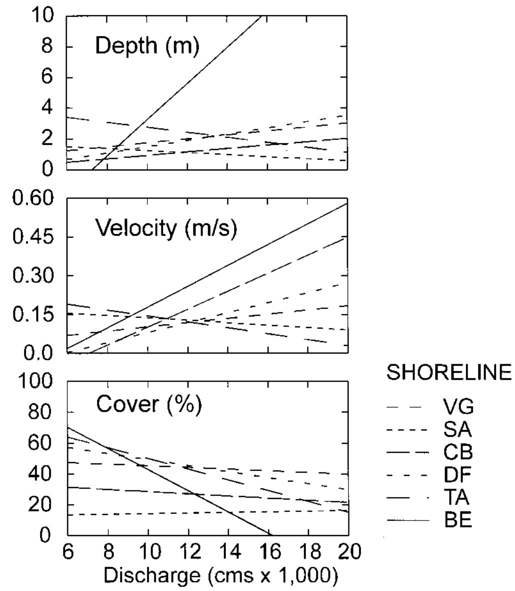

Figure 7. Change in depth, velocity and cover with discharge for each shoreline type. Data points are not shown to facilitate visualization of trends. Be, bedrock; CB, cobble; DF, debris fan; SA, sand; TS, talus; and VG, vegetation

The importance of cover as an attribute of habitat

Numerous studies have demonstrated the importance of cover as a habitat attribute (Fraser and Cerri, 1982; Fraser, 1983; Power *et al.*, 1985; Schlosser, 1987). Cover may be important for several reasons. First, fish may seek out cover to avoid light (Lewis, 1969; Cunjak, 1988). This possibility seems likely for native fish of the Colorado River, which evolved under turbid conditions and have been noted as negatively phototactic (Valdez *et al.*, 1992). Secondly, small fish may find it easier to avoid predation in areas with greater cover (Fraser and Emmons, 1984; Mesick, 1988). The recent introduction of nonnative salmonids, catfish and other piscivorous sport fish has added a substantial source of predation that did not exist historically (Marsh and Douglas, 1994; Valdez and Ryel, 1995). Also, cover is frequently the result of some laterally or vertically emergent object that obstructs flow, thereby providing refuge from high current velocities (Fausch, 1984; McMahon and Hartman, 1989).

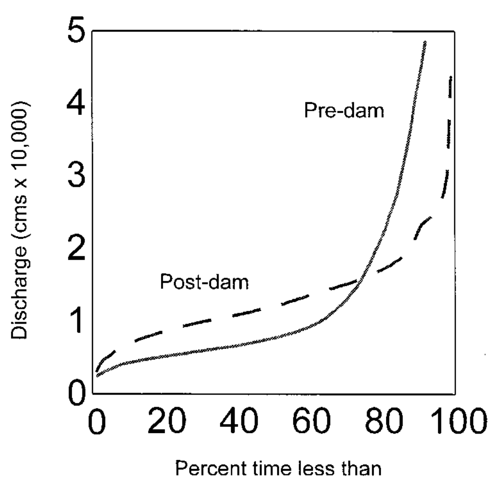

Figure 8. Flow duration curve of the Colorado River at Lee's Ferry gauge

In this study, the association with cover is stronger than those with water velocity or depth in channel margins. However, addressing the biological basis for the strong association with cover was beyond the scope of this study. We suspect that the presence of cover affects local conditions of water depth and velocity in channel margins. However, the distance of 2.5 m used in this study as a boundary for habitat measurements along channel margins may have been too broad to detect associations between fish and specific conditions of depth and velocity. Small fish are probably responding to conditions within 0.5–1 m of the water's edge. If so, a stronger association between fish and velocity or depth may have been masked by main channel hydraulic conditions. A better approach would be to analyze the physical conditions only within the channel margin area that subadult humpback chub use, which may vary among shoreline types, rather than a specific distance from shore.

Historic and present habitat condition

This study also demonstrated that mean depth, velocity and cover of shorelines vary with discharge during base-flow conditions. Consequently, higher base flows, which occur a greater proportion of the time in the current flow regime, may reduce subadult humpback chub habitat quality in natural habitats compared with the same during pre-dam conditions in the Colorado River through Grand Canyon. Reduced habitat quality may partially explain why subadults now use naturalized habitats, like vegetated shorelines, which did not exist historically more than they use natural habitats like talus and debris fan shorelines.

Vegetated shoreline habitat. Shoreline vegetation in Grand Canyon consists mainly of overhanging tamarisk (*Tamarix chinensis*) that has stabilized sand deposits. Tamarisk is an exotic riparian plant that has been present in the Colorado River since the early part of this century but was not able to stabilize sand at the water's edge until the onset of flow regulation in 1962. Before that time, annual floods scoured shorelines of any perennial vegetation, leaving extensive sand beaches (Turner and Karpiscak, 1980).

Relatively high use of vegetated shorelines by subadult humpback chub implies that subadults may prefer these new areas over natural habitats, like talus or debris fans. Naturalized vegetation may be used more than natural habitats for three reasons: (1) original shoreline conditions may have been modified by flow regulation such that they currently provide only marginally acceptable conditions; (2) previously important shoreline types are no longer present; or (3) vegetated shorelines simply provide better habitat conditions than what naturally exist. Another possibility is that a combination of these conditions exists.

Modified shoreline conditions. Flow regulation may alter a suite of physical or biological shoreline conditions, thereby limiting subadult humpback chub habitat quality. Changes in discharge cause basic hydraulic changes in the river (Leopold *et al*., 1964). Before dam operations, base flows of the Colorado River were two to five times less than the current average base flow. These results suggest that higher base flows in the current flow regime increase mean depth and velocity and decrease cover. At-a-station hydraulic geometry predicts that depth and velocity increase as discharge increases (Richards, 1977); however, it is unclear why the occurrence of cover decreases with increasing discharge.

An examination of the cover/discharge relationship for individual shoreline types partially explains this phenomenon. The presence of cover is the result of structural heterogeneity along the wetted perimeter of the channel. The structure of bedrock, debris fan and talus shoreline types depends on morphology of local geology and the shoreline angle of repose along the water's edge. These are geologically dependent shoreline types. As basic geomorphology predicts (Leopold *et al*., 1964; Ritter, 1978), the angle of repose decreases as colluvium accumulates at the toe of the slope. At higher discharges, the channel margins may encounter more uniform or massive colluvium and higher angles of repose, or shoreline availability may shift to more bedrock and sheer walls; consequently, structural heterogeneity would decrease with increasing discharge among these shoreline types.

In contrast, cobble, sand and vegetation shoreline types are formed from main channel activity at high discharges and are exposed as water levels recede. The structure of these shorelines is not as dependent on local lithology; therefore, these shorelines are geologically independent. Because these shorelines are formed by alluvial deposits, their structure and angle of repose at the water's edge is more homogeneous

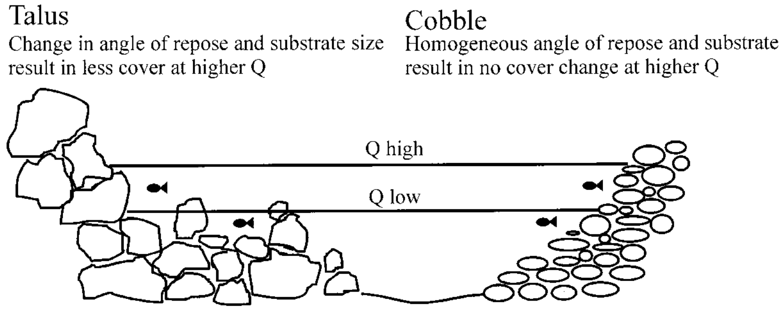

Figure 9. Channel cross section demonstrating difference of how cover changes with discharge between geologically dependent and independent shoreline types

at all discharges encountered in this study (Figure 9). However, this relationship must be sinusoidal over a larger range of discharge, because cobble, sand and vegetation will be exposed at some discharge lower and inundated at some discharge higher than those observed in this study.

Although food abundance was not considered in this study, regulation by Glen Canyon Dam has altered food availability and the food web dynamics in the Colorado River through Grand Canyon (Blinn and Cole, 1991; Angradi, 1994). Glen Canyon dam traps allochthonous debris, thereby shifting the food base from allochthonous to primarily autochthonous material. Such alterations may alter or limit food availability in channel margins. However, vegetated shorelines may provide allochthonous debris from riparian vegetation and, macroinvertebrates may be associated with such inputs. Fish may select vegetation for this reason only, or more likely, they may be attracted to a combination of habitat conditions that include greater food availability and specific physical conditions.

Loss of historic habitat. Another possible explanation for subadult humpback chub occurring along vegetated shorelines rather than natural shoreline types is that certain habitat types have been lost with the onset of flow regulation. Because flow and sediment transport regimes in the Colorado River through Grand Canyon have been altered, sand deposits are less extensive and structurally more simple (less sinuous perimeter and less complex bedforms) than those that occurred in the pre-dam era (Graf *et al.*, 1987; Schmidt and Rubin, 1995). Sand deposits may have historically provided complex, sinuous shoreline habitat, such as backwater habitat, that no longer exists or is currently infrequent and ephemeral. Shoreline complexity in sand deposits (e.g. backwater habitat) is known to provide lower depths and velocities for small fish and greater protection from predators (Tyus, 1991, 1991; Jurajda, 1995). The few backwaters that are permanent in Grand Canyon can have very high densities of young native fish, but fish presence in backwaters depends on high turbidity conditions (personal observation; Arizona Game and Fish Department, 1994; Valdez and Ryel, 1995).

Implications of flow regulation on survival of subadult humphack chub

When compounded with other changes in the river ecosystem, decreased habitat quality may limit survival of subadult humpback chub in Grand Canyon. In addition to a general reduction in physical habitat quality, the dam has altered water temperature. Historically, temperatures ranged from 2 to 18°C. The Colorado River temperature now averages from 9 to 11°C at the LCR (US Department of Interior, Bureau of Reclamation, 1995; Valdez and Ryel, 1995). Consequently, growth, reproduction and survival of native fish have almost certainly been affected. Bulkley *et al.* (1981) showed extreme compromises in swimming abilities and growth rates of humpback chub in temperatures ranging from 5 to 15°C. In response to these changes in the wild, young fish may be limited to very different environments where they expend less energy to compensate for reduced growth efficiency imposed by suboptimal temperatures. For example, subadult humpback chub may be forced to occupy a portion of the channel margin nearer to shore, which has more cover and refuge from high velocities to reduce energy expenditure, or young fish may shift to naturalized vegetated shorelines that consistently provide these conditions at a range of discharges.

These thermal constraints together with a decrease in habitat quality due to artificially high base flows and a change in food availability have probably inflicted an extreme and detrimental post-dam environmental change on subadult humpback chub in the Colorado River through Grand Canyon that limits their growth and survival. Yet, to date, the effect of artificially elevated base flows has not been adequately included in the evaluation of Glen Canyon Dam operations on native fish habitat in the Colorado River through Grand Canyon.

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